AYESSA MICHELLE ROSA DE OLIVEIRA CALDERANO

REDES DE INTERAÇÕES ENTRE BESOUROS CIIDAE E SEUS FUNGOS HOSPEDEIROS EM FRAGMENTOS FLORESTAIS DE VIÇOSA, MINAS GERAIS

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Biologia Animal para obtenção do título de *Magister Scientiae*.

Orientador: Cristiano Lopes Andrade

Coorientadora: Lucimar Soares de Araujo

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RESUMO

ROSA-OLIVEIRA, Ayessa, M.Sc., Universidade Federal de Viçosa, fevereiro de 2022. **Redes de interações entre besouros Ciidae e seus fungos hospedeiros em fragmentos florestais de Viçosa, Minas Gerais.** Orientador: Cristiano Lopes Andrade. Coorientadora: Lucimar Soares de Araujo.

A micofagia, hábito de se alimentar de estruturas fúngicas ou de material vegetal que tenha sido decomposto por enzimas fúngicas, é um dos hábitos alimentares mais antigos dos besouros. Uma importante família de besouros que possuem associação obrigatória com fungos é Ciidae, cujos integrantes utilizam os fungos como abrigo e alimento durante todo seu ciclo de vida, sendo classificados como micetobiontes. Os fungos aos quais os ciídeos se associam pertencem ao filo Basidiomycota e apresentam importante papel na ciclagem de nutrientes, pois realizam degradação da madeira, sendo capazes de decompor celulose, hemicelulose e lignina. Os ciídeos são responsáveis pela degradação de grande parte dos basidiomas desses fungos, impedindo maior acúmulo dessas estruturas e contribuindo com o aumento da disponibilidade de nutrientes importantes para os sistemas florestais. Embora as interações entre os besouros Ciidae e seus fungos hospedeiros já tenham sido relativamente bem estudadas, os estudos dessas interações na região Neotropical ainda são escassos. Diante disto, realizamos neste trabalho, um estudo das interações dos ciídeos e seus hospedeiros em dois fragmentos florestais pertencentes ao bioma Mata Atlântica. Utilizamos a abordagem de análise de redes ecológicas e avaliamos importantes índices usados para descrever comunidades: conectância, assimetria da rede, links por espécie, aninhamento, robustez e especialização. Assim, foi possível conhecer e comparar as estruturas das duas comunidades de Ciidae e seus fungos hospedeiros. Nossos resultados mostraram que as principais espécies de fungos hospedeiros das duas comunidades foram as mesmas. Apesar disso, encontramos diferenças no uso de hospedeiros pelos ciídeos de acordo com a disponibilidade de espécies fúngicas, resultando em diferentes estruturas de rede. Encontramos espécies de Ciidae que nos permitiram fazer importantes inferências a respeito da qualidade dos fragmentos estudados.

Keywords: Ciidae. Micetobiontes. Micofagia. Rede de interação.

ABSTRACT

ROSA-OLIVEIRA, Ayessa, M.Sc., Universidade Federal de Viçosa, February, 2022. **Interaction networks between Ciidae beetles and their host fungi in forest remnants of Viçosa, Minas Gerais.** Advisor: Cristiano Lopes Andrade. Co-advisor: Lucimar Soares de Araujo.

Mycophagy, the habit of feeding on fungal structures or plant material that has been decomposed by fungal enzymes, is one of the oldest feeding habits of beetles. An important family of beetles that have an obligatory association with fungi is Ciidae, whose members use fungi as shelter and food throughout their life cycle, being classified as mycetobionts. The fungi to which ciids are associated belong to the phylum Basidiomycota and play an important role in nutrient cycling, as they perform wood degradation, being able to decompose cellulose, hemicellulose and lignin. Ciidae are responsible for the degradation of most of the basidiomes of these fungi, preventing further accumulation of these structures and contributing to the increase in the availability of important nutrients for forest systems. Although interactions between Ciidae beetles and their host fungi have already been relatively well studied, studies of these interactions in the Neotropics are still scarce. In view of this, in this work, we carried out a study of the interactions of ciids and their hosts in two forest remnants belonging to the Atlantic Forest biome. We used the approach of ecological network analysis and evaluate important indices used to describe communities: connectance, web asymmetry, links per species, nestedness, robustness and specialization. Thus, it was possible to know and compare the structures of the two communities of Ciidae and their host fungi. Our results showed that the main host fungal species of the two communities were the same. Despite this, we found differences in the use of hosts by ciids according to the availability of fungal species, resulting in different network structures. We found species of Ciidae that allowed us to make important inferences about the quality of the fragments studied.

Keywords: Ciidae. Mycetobionts. Mycophagy. Network. Bipartite.

SUMÁRIO

INTRODUÇÃO GERAL

Os besouros (Insecta: Coleoptera) constituem a ordem com a maior biodiversidade entre os animais, apresentando cerca de 420.000 espécies descritas (ŚLIPIŃSKI, LESCHEN & LAWRENCE, 2011). Essa grande biodiversidade do grupo decorre possivelmente das altas taxas de persistência das suas linhagens evolutivas e da diversificação em uma ampla variedade de nichos (HUNT *et al.*, 2007), já que exploram vários tipos de habitats e apresentam diferentes hábitos alimentares (LAWRENCE & ŚLIPIŃSKI, 2013).

Os besouros têm grande importância ecossistêmica, atuando, por exemplo, como polinizadores, herbívoros, detritívoros e predadores, e servindo de alimento para outros animais (LEWINSOHN & PRADO, 2005). Isso permite a utilização desses insetos para estimar de forma indireta a biodiversidade dos organismos com os quais interagem, como fungos, plantas e vertebrados (HUNT *et al.*, 2007). Assim, é possível obter informações robustas que podem ser utilizadas para avaliar impactos ambientais e sugerir medidas conservacionistas.

Um dos hábitos alimentares mais antigos dos besouros é a micofagia (LAWRENCE, 1989) ou fungivoria (HANSKI, 1989), hábito de se alimentar de estruturas fúngicas ou de material vegetal que tenha sido decomposto por enzimas fúngicas (LAWRENCE, 1989). A especialização em micofagia foi uma forte pressão seletiva na evolução de adaptações morfológicas, fisiológicas e de ciclo de vida de besouros (LAWRENCE, 1989). Foram observadas adaptações do aparelho bucal desses animais (LAWRENCE, 1989), com presença de mandíbulas desenvolvidas nas larvas (PAVIOUR-SMITH, 1960), além de adaptações do aparelho ovipositor e do ciclo reprodutor (LAWRENCE, 1989). Essas modificações podem ser relacionadas à estrutura e consistência dos fungos hospedeiros, já que fungos coriáceos e persistentes permitem pupação interna com maior tempo de desenvolvimento larval (LAWRENCE, 1989; DELGADO-CASTILLO & NAVARRETE-HEREDIA, 2011); enquanto observa-se cuidado parental e pupação no solo dos besouros que se alimentam de fungos moles e de vida curta (DELGADO-CASTILLO & NAVARRETE-HEREDIA, 2011). Além dessas adaptações, os besouros fungívoros são capazes de reconhecer compostos voláteis liberados pelos fungos hospedeiros e desenvolveram um mecanismo fisiológico que permite se alimentar e reproduzir nesses fungos (GUEVARA, *et al.*, 2000).

Uma importante família de Coleoptera em que as espécies são, em sua maioria, associadas a fungos é Ciidae (Tenebrionoidea). Ciidae é mundialmente distribuída e bastante diversa, com cerca de 750 espécies descritas, agrupadas em 51 gêneros (LAWRENCE & LOPES-ANDRADE, 2010; LAWRENCE, 2016; SOUZA-GONÇALVES *et al.*, 2018, SOUZA-GONÇALVES *et al.*, 2020), sendo que cerca de 160 espécies pertencentes a 14 gêneros ocorrem na região Neotropical (classificação biogeográfica segundo MORRONE, 2014). Os ciídeos são pequenos besouros (0,5 a 7 mm) em que imaturos e adultos apresentam associação obrigatória com basidiomas de fungos poliporoides (PAVIOUR-SMITH, 1960; ORLEDGE & REYNOLDS, 2005). São, por isso, classificados como micetobiontes, animais cujo ciclo de vida depende completamente dos fungos, onde estes servem de abrigo e alimento para larvas e adultos, além de local de cópula e oviposição (HAMMOND & LAWRENCE, 1989; NAVARRETE-HEREDIA & MIRANDA, 1997).

Os ciídeos estão entre os besouros micófagos mais abundantes (LAWRENCE, 1973; GRAF-PETERS *et al.*, 2011) e se associam a macrofungos pertencentes ao filo Basidiomycota, especialmente das ordens Polyporales e Hymenochaetales (PAVIOUR-SMITH, 1960; ORLEDGE & REYNOLDS, 2005; LAWRENCE & LOPES-ANDRADE, 2010), cujos integrantes formam estruturas reprodutivas (basidiomas) com himenóforo poroide (WEBSTER & WEBER, 2007) e são popularmente conhecidos como “orelhas-de-pau”. Os fungos orelha-de-pau apresentam importante papel na ciclagem de nutrientes (GIBERTONI *et al.*, 2015), pois são predominantemente saprotróficos (RYVARDEN &

MELO, 2014) e realizam degradação de madeira, sendo capazes de decompor celulose, hemicelulose e lignina (SCHIGEL, 2016; WEBSTER & WEBER, 2007).

Ao realizar a decomposição da matéria orgânica, os macrofungos de madeira se tornam importantes fontes de proteínas e carboidratos para os insetos (HSU *et al.*, 2002; SCHIGEL, 2011). Entretanto, esses não são recursos homogêneos, visto que os nutrientes se concentram especialmente em seus basidiomas (HSU *et al.*, 2002; SCHIGEL, 2009). Nos basidiomas desses macrofungos concentram-se principalmente carbono e nitrogênio, encontrando-se também fósforo, potássio e outros nutrientes (MARTIN, 1979; WATKINSON *et al.*, 2006). Os basidiomas também podem concentrar toxinas, o que gerou possivelmente uma pressão seletiva para que os ciídeos desenvolvessem mecanismos fisiológicos de resistência a toxinas presentes nos fungos hospedeiros (MARTIN, 1979).

Devido à sua consistência e maior resistência, os macrofungos coriáceos formam basidiomas que persistem por mais tempo no ambiente, se comparados aos cogumelos (JONSELL *et al.*, 2001; YAMASHITA *et al.*, 2015), mesmo depois de mortos (PAVIOUR-SMITH, 1960). Isso permitiu a especialização dos ciídeos em completar todo o ciclo de vida dentro dos fungos (JONSELL & NORDLANDER, 2004), além de manter várias gerações em um mesmo basidioma (LAWRENCE, 1973; HANSKI, 1989). Sendo responsáveis pela degradação de grande parte desses basidiomas (LAWRENCE, 1973), impedindo maior acúmulo dessas estruturas no ambiente, os ciídeos contribuem com o aumento da disponibilidade de nutrientes importantes para os sistemas florestais (THUNES *et al.*, 2000).

Por serem extremamente dependentes dos basidiomas, os ciídeos são sensíveis a quaisquer alterações ambientais que possam afetar o desenvolvimento desses macrofungos (THUNES *et al.*, 2000), como por exemplo a fragmentação florestal, que reduz a disponibilidade de madeira em decomposição (ARAUJO *et al.*, 2015). Essa relação de dependência dos fungos torna os ciídeos, junto aos outros organismos micetobiontes, mais vulneráveis à extinção, se não houver conservação das áreas nativas.

Ainda que as interações entre ciídeos e fungos orelha-de-pau tenham sido relativamente bem estudadas (JONSELL & NORDLANDER, 2004; KOMONEN, 2003; LAWRENCE, 1973; ORLEDGE & REYNOLDS, 2005; SCHIGEL, 2011, 2012), estudos com espécies neotropicais são incipientes (GRAF-PETERS *et al.*, 2011; YAMASHITA *et al.*, 2015), possivelmente por falta de informação a respeito dos macrofungos coriáceos da região (YAMASHITA *et al.*, 2015). Um estudo realizado em localidades pertencentes ao Cerrado e à Mata Atlântica apresentou uma busca por padrões de utilização de fungos hospedeiros por espécies de ciídeos, porém obtiveram baixa amostragem em cada fragmento (ARAUJO, 2014). Em Graf (2008) e Graf *et al.* (2018), encontramos estudos de fatores que influenciam a interação de espécies de besouros e fungos, como a taxonomia, filogenia e consistência dos fungos; entretanto, esses estudos não enfatizaram Ciidae.

Uma importante ferramenta empregada em estudos de ecologia de comunidades é a análise de redes de interações ecológicas (BLÜTHGEN *et al.*, 2008). Esse método permite descrever como as espécies se relacionam (PIMM, 1980) e investigar suas funções no ecossistema (BASCOMPTE *et al.*, 2006), além de ser muito útil na avaliação de processos ambientais como restauração e recuperação de habitats (FORUP *et al.*, 2008). Na abordagem de redes de interações é possível avaliar diversas métricas das comunidades, sejam elas qualitativas ou quantitativas (BLÜTHGEN *et al.*, 2008). Por meio dessas métricas, é possível conhecer a estrutura das comunidades, os padrões de especialização ou generalização das espécies e os fatores que promovem a estabilidade da comunidade (BASCOMPTE *et al.*, 2006).

A abordagem de redes de interações já foi utilizada na estimativa de alterações em comunidades de diversos sistemas como, por exemplo, hospedeiro-parasitoide

(TYLIANAKIS *et al.*, 2007) e polinizador-planta (FORUP *et al.*, 2008). Entretanto, seu uso em estudos das interações entre besouros e fungos é escasso (SCHIGEL, 2011). Em um trabalho recente, Kobayashi & Sota (2021) estudaram as interações entre os ciídeos do Japão e seus hospedeiros por meio de dados moleculares, analisando as relações filogenéticas entre os principais grupos de Ciidae e a história evolutiva do uso dos fungos. Contudo, a pesquisa não envolveu análise de rede de interações.

Uma análise de redes de interações entre besouros fungívoros e macrofungos de uma comunidade de floresta tropical pode ser encontrada no trabalho de Yamashita *et al.* (2015), porém foi realizada uma baixa amostragem de espécies de Ciidae. Também podemos citar a dissertação de mestrado de Mezzomo (2018), que utilizou análise de redes de interação entre besouros e macrofungos hospedeiros para avaliar processos de restauração de localidades, sem foco nos ciídeos.

OBJETIVOS E JUSTIFICATIVAS

Diante da escassez de estudos de interações entre besouros Ciidae e seus fungos hospedeiros na região Neotropical, e do potencial uso da metodologia de análise de redes para estudo dessas interações, realizamos a presente pesquisa visando conhecer e comparar a estrutura de comunidades de ciídeos e fungos hospedeiros de localidades pertencentes ao bioma Mata Atlântica.

Utilizamos o método de análise de redes para conhecer a estrutura das comunidades de ciideos e fungos hospedeiros de dois fragmentos florestais localizados no município de Viçosa, Minas Gerais. As áreas estudadas, conhecidas como “Mata da Biologia” e “Mata do Paraíso”, são fragmentos de floresta estacional semidecidual que se encontram em processo natural de regeneração.

Nossos objetivos específicos no presente trabalho são:

1) Elucidar as redes de interações entre besouros ciídeos e fungos orelha-de-pau em dois fragmentos florestais;

2) Detectar possíveis diferenças entre as estruturas dessas redes de interações nos dois fragmentos florestais amostrados.

METODOLOGIA, RESULTADOS E DISCUSSÃO

Os métodos, resultados e discussão são apresentados no capítulo único que se segue, na forma de um manuscrito de artigo científico a ser submetido para a revista Ecology and Evolution.

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INTERACTION NETWORKS OF CIIDAE-HOST FUNGI OF ATLANTIC FOREST REMNANTS IN SOUTHEAST BRAZIL

(Ecology and Evolution)

INTERACTION NETWORKS CIIDAE-HOST FUNGI OF ATLANTIC FOREST REMNANTS IN SOUTHEAST BRAZIL

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ABSTRACT

Mycophagy, the habit of feeding on fungal structures or plant material that has been decomposed by fungal enzymes, is one of the oldest feeding habits of beetles. An important family of beetles that have an obligatory association with fungi is Ciidae, whose members use fungi as shelter and food throughout their life cycle, being classified as mycetobionts. The fungi to which ciids are associated belong to the phylum Basidiomycota and play an important role in nutrient cycling, as they perform wood degradation, being able to decompose cellulose, hemicellulose and lignin. Ciidae are responsible for the degradation of most of the basidiomes of these fungi, preventing further accumulation of these structures and contributing to the increase in the availability of important nutrients for forest systems. Although interactions between Ciidae beetles and their host fungi have already been relatively well studied, studies of these interactions in the Neotropics are still scarce. In view of this, in this work, we carried out a study of the interactions of ciids and their hosts in two forest remnants belonging to the Atlantic Forest biome. We used the approach of ecological network analysis and evaluate important indices used to describe communities: connectance, web asymmetry, links per species, nestedness, robustness and specialization. Thus, it was possible to know and compare the structures of the two communities of Ciidae and their host fungi. Our results showed that the main host fungal species of the two communities were the same. Despite this, we found differences in the use of hosts by ciids according to the availability of fungal species, resulting in different network structures.

Keywords: Ciidae, mycetobionts, mycophagy, network, bipartite

INTRODUCTION

One of the oldest feeding habits of Coleoptera is mycophagy (LAWRENCE, 1989), also called fungivory (HANSKI, 1989), the habit of feeding on fungal structures or plant material that has been decomposed by fungal enzymes (LAWRENCE, 1989). An ecologically important Coleoptera family in which the species are mostly associated with fungi is Ciidae (Coleoptera: Tenebrionoidea), comprising about 750 described species of tiny beetles (0.5–7 mm long) grouped into 51 genera (LAWRENCE & LOPES-ANDRADE, 2010; LAWRENCE, 2016; SOUZA-GONÇALVES *et al.*, 2018, SOUZA-GONÇALVES *et al.*, 2020). The taxonomic knowledge on the Neotropical ciids is incipient, with 160 described species of 14 genera known from the region.

Ciids are among the most abundant fungivorous beetles (LAWRENCE, 1973; GRAF-PETERS et al., 2011) and use the basidiomes of fungi in all their developmental stages (PAVIOUR-SMITH, 1960), as shelter and food, being then classified as mycetobionts (HAMMOND & LAWRENCE, 1989; NAVARRETE-HEREDIA & MIRANDA, 1997). These beetles have an obligatory association with macrofungi belonging to the phylum Basidiomycota, especially of the orders Polyporales and Hymenochaetales (PAVIOUR-SMITH, 1960; ORLEDGE & REYNOLDS, 2005; LAWRENCE & LOPES-ANDRADE, 2010), whose members form reproductive structures (basidiomes) with poroid hymenophores (WEBSTER & WEBER, 2007).

These macrofungi play an important role in nutrient cycling (GIBERTONI et al., 2015), as they are predominantly saprotrophic (RYVARDEN & MELO, 2014) and perform wood degradation, being able to decompose cellulose, hemicellulose and lignin (SCHIGEL, 2016; WEBSTER & WEBER, 2007). When carrying out the decomposition of organic matter, these fungi become important sources of proteins and carbohydrates for insects (HSU et al., 2002;

SCHIGEL, 2011). However, these are not homogeneous resources, as the nutrients are especially concentrated in their basidiomes (HSU et al., 2002; SCHIGEL, 2009).

Due to their consistency and greater resistance, bracket fungi have basidiomes that persist longer in the environment, compared to mushrooms (JONSELL et al., 2001; YAMASHITA et al., 2015), even after death (PAVIOUR-SMITH, 1960). Ciids, being responsible for the degradation of a large part of these basidiomes (LAWRENCE, 1973), prevent greater accumulation of these structures in the environment, contributing to the increased availability of important nutrients for forest systems (THUNES et al., 2000).

Although interactions between ciids and host fungi have been relatively well studied (JONSELL & NORDLANDER, 2004; KOMONEN, 2003; LAWRENCE, 1973; ORLEDGE & REYNOLDS, 2005; SCHIGEL, 2011, 2012), these studies in the neotropics are incipient (GRAF-PETERS et al., 2011; YAMASHITA et al., 2015), possibly due to the scanty information about the coriaceous macrofungi in the region (YAMASHITA et al., 2015).

An important tool used in community ecology studies is the analysis of ecological interaction networks (BLÜTHGEN et al., 2008). This method allows describing the relationships between species (PIMM, 1980) and investigating their ecosystem functions (BASCOMPTE et al., 2006), in addition to being very useful in the assessment of environmental processes such as habitat restoration and recovery (FORUP et al., 2008). The analysis of networks allows knowing the structure of communities, the patterns of specialization or generalization of species and the factors that promote community stability (BASCOMPTE et al., 2006).

The trophic network approach has already been used to estimate changes in communities in different systems, such as host-parasitoid (TYLIANAKIS et al., 2007) and plant-pollinator (FORUP et al., 2008). However, its use in studies of the interaction between beetles and fungi is scarce (SCHIGEL, 2011). Given the lack of studies of these interactions in the Neotropical region and the potential use of network analysis methodology, we seek here to know the structure of ciid communities and their hosts in two forest remnants of the Atlantic Forest biome. The remnants, of different sizes, had in their history different periods and degrees of human intervention and are in a natural process of regeneration.

Relying on the importance of environmental and landscape factors on the biodiversity of ciid beetles within forested areas, we tested the following assumptions: 1) interaction networks between species of ciid beetles and bracket fungi may vary between forest remnants, revealing distinct local community structures; 2) ciid species within these remnants may have distinct degrees of specialization to host fungi.

MATERIAL AND METHODS

Study sites

The collections were carried out in two remnants of Atlantic Forest located in the municipality of Viçosa, Minas Gerais (Fig. 1), currently belonging to the Federal University of Viçosa: “Mata da Biologia” (20°48’05” S, 42°51’58” W); and “Estação de Pesquisa, Treinamento e Educação Ambiental Mata do Paraíso” (20°45’32” S, 42°51’49” W). Both are remnants of seasonal semideciduous forest in a natural regeneration process.

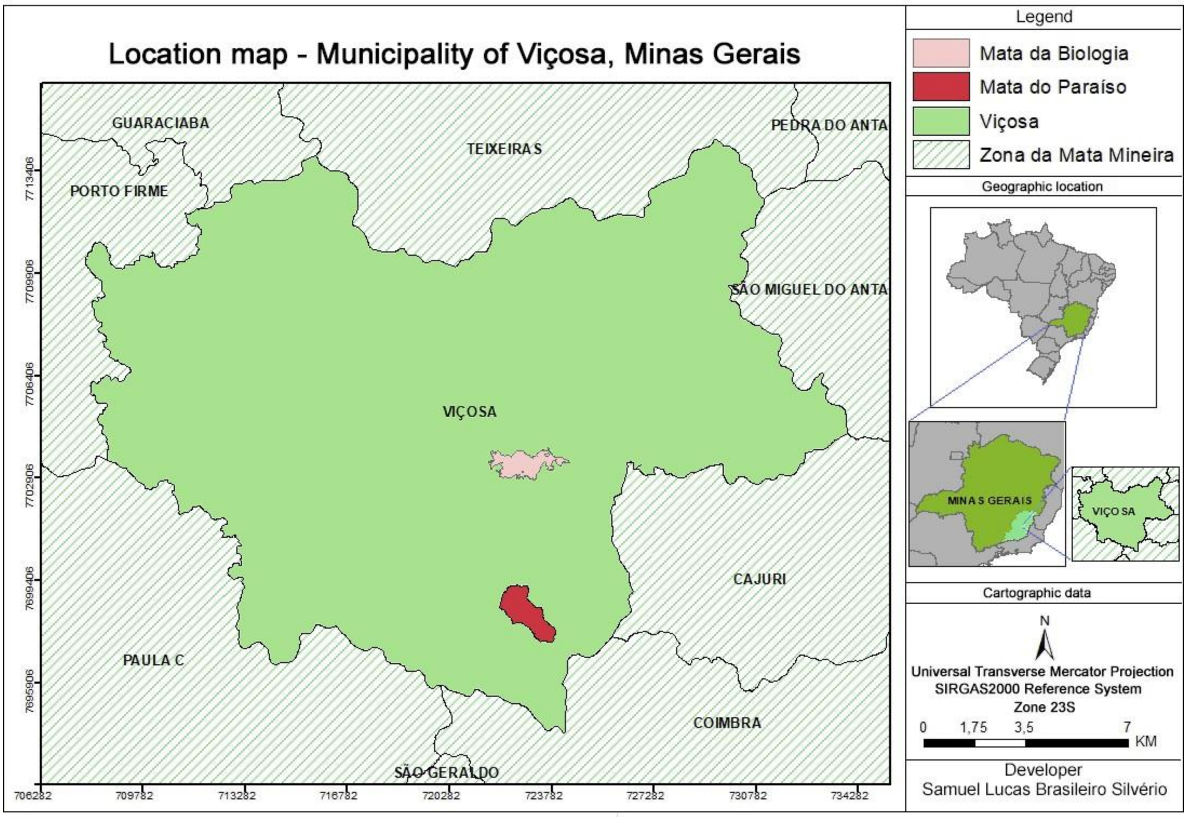

Figure 1. Location map of the studied remnants.

Mata da Biologia (hereafter MB; Fig. 2) include about 75 ha and had its regeneration process started in 1926, after a long period of coffee cultivation and wood extraction (FERREIRA JUNIOR *et al.*, 2007). Despite being in an advanced stage of recovery, the remnant suffers a high edge effect due to the extreme urbanization on its banks, with traffic lanes for cars and pedestrians, and several buildings. Mata do Paraíso (hereafter MP; Fig. 3) has an area of about 195 ha under strict use (mainly for environmental education and scientific researches), but is surrounded by private forested areas, totaling 384 ha of continuous forest cover. Its regeneration process began in 1963, with the end of its use for pasture in some areas and wood exploration (SILVA-JUNIOR *et al.*, 2004).

Figura 2. Entrance of the rainforest remnant Mata da Biologia.

Figure 3. Entrance of the rainforest remnant Mata do Paraíso.

Field collections, maintenance and identification of basidiomes

Trails that already existed in the forest remnants were used as a reference for collections. Active searches for bracket fungi were carried out through arbitrary walks, checking dead logs, turning them whenever necessary and returning them to the initial position afterwards. We have also paid attention to the presence of bracket fungi in standing logs or even alive trees. We prioritized collecting basidiomes with small visible holes, indicating the presence ciids or other mycophagous beetles (Fig. 4D). We avoid very young and the largest persistent basidiomes (GRAF-PETERS *et al.*, 2011).

The basidiomes were photographed in the field, temporarily stored in properly identified paper bags and taken to the Laboratório de Sistemática e Biologia de Coleoptera da UFV (LabCol). There they were transferred to plastic pots containing silica and covered by perforated lid, where they were kept for about two months. During this period, the pots were kept under controlled humidity to allow the development of ciids, aiming to obtain a great number of individuals (GRAF-PETERS *et al.*, 2011).

The fungi were identified at the lowest possible taxonomic level with the help of photographic records and the available literature (e.g. GUZMÁN & PIEPENBRING, 2011; MEIJER, 2008, NEVES *et al.*, 2013; WRIGHT & ALBERTÓ, 2006) and scientific names were verified and updated in the Index Fungorum database (http://www.indexfungorum.org/).

Figure 4. Examples of host fungi. **A.** Individual of *Datronia caperata* with several basidiomes. **B.** Basidiomes of *Bjerkandera adusta*. **C.** Basidiome of *Trametes villosa*. **D.** Basidiome with holes (red arrows) made by ciid beetles.

Breeding, sorting and identification of ciids

Two months after being collected, each basidiome was fragmented and all adult beetles found were extracted and preserved in absolute ethanol. Them the specimens were sorted and the ciids were double-mounted in insect pins, labelled and organized in morphospecies. Identification was made to the lowest possible taxonomic level, by comparison to the reference collection of ciids of the LabCol and by consulting the pertinent taxonomic papers, especially those with identification keys (e.g. LAWRENCE, 1971; LOPES-ANDRADE & LAWRENCE, 2011; LOPES-ANDRADE, 2008; OLIVEIRA *et al.*, 2013; PECCI-MADDALENA & LOPES-ANDRADE, 2017; SOUZA-GONÇALVES *et al.*, 2018). All specimens of the present study were deposited in the scientific collection of the LabCol.

Criteria for determining host fungi

Some arbitrary criteria are adopted to consider a fungus species as a host, and these varied between authors, especially concerning the minimum number of ciid beetles in each individual fungus (LAWRENCE, 1973; ORLEDGE & REYNOLDS, 2005). In the present study, we have taken into account only the samples with two or more individuals of adult ciid beetles.

Interaction networks and data analysis

Data from each forest remnant were used separately to assemble weighted interaction matrices, where the columns represented the higher trophic level species (beetles) and the rows represented the lower trophic level species (fungi). Thus, samples of fungi not colonized by ciids were excluded from the analysis. The matrix cells were filled with 0, in the absence of interaction, and numbers greater than 0, according to the frequency of occurrence of ciid species in the fungus species.

All analyzes were performed using the *bipartite* package version 2.15 of the R *software* (R Statistical Environment version 4.0.3; 2020-10-10), which provides functions to visualize bipartite networks and calculate indices describing ecological networks (DORMANN *et al.*, 2015). With the “visweb” function, matrices were drawn (Figs 8, 9), representing the number of interactions per link through shading. With the “plotweb” function, bipartite networks were drawn (Figs 10, 11), where the species are represented by rectangles of width proportional to the sum of their interactions occurring and the lines represent the interactions.

We analyze the structure of communities by calculating important indices of metrics commonly used to describe patterns in ecological webs, using the “networklevel” function. We paid attention to the following metrics: connectance, web asymmetry, links per species, nestedness, robustness and specialization. Connectance measures the complexity of the network showing the proportion of possible interactions between species realized (PIMM, 1980; DUNNE *et al.*, 2002). Web asymmetry shows the balance of the number of species at the two levels (BLÜTHGEN *et al.*, 2007). Links per species is the average number of links per species.

Nestedness is a species distribution pattern, related to species diversity, and we calculate it using the method WNODF-metric (Weighted Nestedness Metric Based on Overlap and Decreasing Fill), which considers the interaction frequencies. Nestedness values range from 0 (not nested) to 100 (perfectly nested) (ALMEIDA-NETO & ULRICH, 2011). The contribution by species to the nesting was estimated using the “nestedcontribution” function, which converts the matrix to binary data and shows which species contribute positively and negatively (SAAVEDRA *et al.*, 2011). Robustness measures the robustness of the system to species loss. Specialization was measured using the H2’ index, which measures specialization at the network level and ranges from 0 for more generalist to 1 for more specialist (DORMANN, 2015).

We adopted the approach of null models (standard with 100 simulations), in order to eliminate size and format effects of the matrices (DORMANN *et al.*, 2009). Through simulations of fungal species loss in the networks, we predicted the secondary extinction of ciid species, using the “second.extint” function. The analyzes were carried out with the aid of scientific works carried out in the area (e.g. ALMEIDA-NETO & ULRICH, 2011; BASCOMPTE *et al.*, 2006; BLÜTHGEN *et al.*, 2008; DORMANN *et al.*, 2008; DORMANN, 2020; GOTELLI, 2000; MIRANDA *et* al., 2019; NICHOLS *et al.*, 2016; PERES-NETO *et al.*, 2001).

RESULTS

We collected basidiomes of 123 individual fungi, of which 95 had ciid beetles (27 from MB and 68 from MP). Adding the species found in the two remnants, we collected 26 different Ciidae species (Figs. 5-7; Tab. 1) and 24 fungus species (examples in Fig 4A-4C; Tab. 2). Four ciid species were found only at MB (*Cis* sp. G, *Cis pallidus,* "*Lipedanicis*"[1] sp. 1 e "*Lipedanicis*" sp. 2) and eight only at MP (*Cis* aff. *setifer*, *Cis* sp. F, *Cis* sp. H, *Grossicis diadematus*, "*Lipedanicis*" sp. 3, *Strigocis vicosensis*, *Porculus dufaui*, and Gen. nov. sp. 1). Among the fungi species, only six were found in both forest remnants: *Bjerkandera adusta*, *Cyclomyces tabacinus*, *Datronia caperata*, *Phellinus gilvus*, *Phellinus* sp. and *Trametes villosa*.

The interaction network of MB (Fig. 10) had 29 species: 18 of the higher trophic level (ciid species) and 11 of the lower trophic level (fungus species). Values of connectance, web asymmetry, links per species, weighted NODF (nestedness) and H2' were 0.19, 0.24, 1.31, 9.28 and 0.33, respectively. The robustness in the higher trophic level was 0.72, and in the lower, 0.64. The interaction network of MP (Fig. 11) had 41 species: 22 species of the higher trophic level and 19 species of the lower. Values of connectance, web asymmetry, links per species, weighted NODF and H2' were 0.14, 0.07, 1.39, 13.85 and 0.42, respectively. The robustness was 0.66 in the higher trophic level and 0.65 in the lower.

The analyses showed that *Ceracis zarathustrai* was the most frequent and the most generalist species at the MB, using five of the 18 host fungus species, followed by *Cis kawanabei*, *C. pubescens* and *Ceracis bicornis*, each using four host fungus species. The most

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[1] Scientific names in quotation marks refer to unpublished names.

generalist species at the MP was *Ce. bicornis*, using seven of the 19 host fungus species, followed by *C. pubescens* and *Ceracis* sp. 1, each using six host fungus species. The host fungus species most used by the greatest number of ciid species (10 species) was *Phellinus gilvus* (Hymenochaetaceae), in both forest remnants.

Cis sp. G provided the greatest contribution to the nestedness of the MB network among species in the higher trophic level (ciids) (1.37), followed by *Falsocis brasiliensis* (1.33) and *Ce. zarathustrai* (1.20), while "*Lipedanicis*" sp. 1 had the lowest contribution (-0.98), followed by *Cis* aff. *bahiensis* (-0.75) and *Ceracis* sp. 1 (gp. *cucullatus*) (-0.68). Among species in the lower trophic level (fungi), the greatest contribution for the nestedness was provided by *Phellinus gilvus* (2.88), followed by *Trametes villosa* (1.11), while *Ganoderma tornatum* provided the lowest contribution (-1.05), followed by *Stereum ostrea* (-0.94). At the MP, the greatest contributions to the nestedness among species in the higher trophic level (ciids) were provided by *C. kawanabei* (1.64) and *C. pubescens* (1.64), followed by *Ce. bicornis* (1.57), while the lowest contribution was provided by *Po. dufaui* (-1.27), followed by "*Lipedanicis*" sp. 3 (-0.97) and *S. vicosensis* (-0.54). In the lower trophic level (fungi), the greatest contribution was provided by *Phellinus* sp. (2.27), followed by *Phellinus gilvus* (1.81) and *Trametes villosa* (1.57), while the lowest contribution was provided by *Cyclomyces tabacinus* (-1.26), followed by *Phellinus fastuosus* (-1.01) and *Phellinus umbrinellus* (-0.94).

The sequential removal of fungus species, from the most to the least connected, showed a linear decrease of ciid species at both MB and MP (Figs 12, 13).

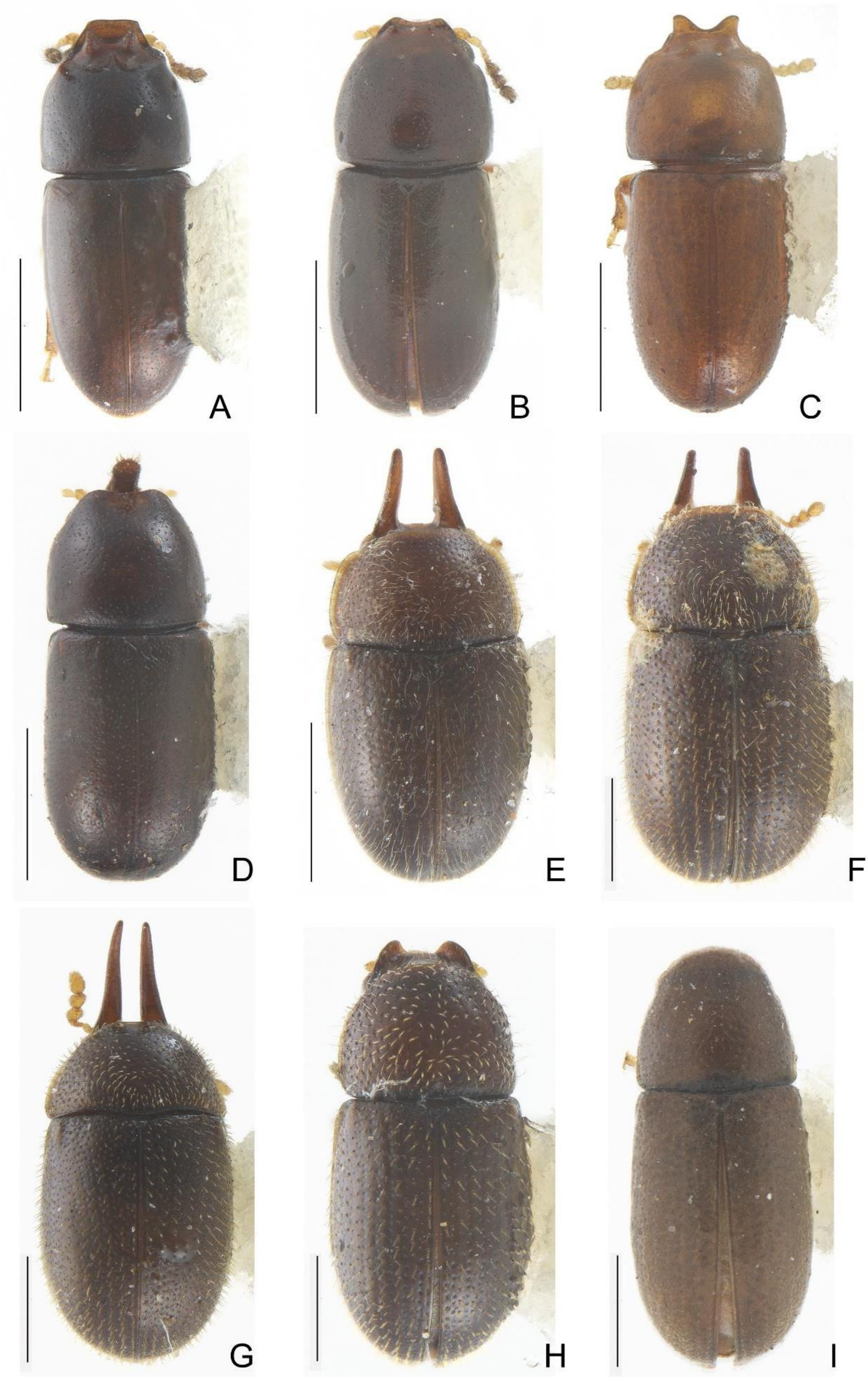

Figure 5. A. *Ceracis bicornis.* **B.** *Ceracis* sp. 1. **C.** *Ceracis limai.* **D.** *Ceracis zarathustrai.* **E.** *Cis* aff. *bahiensis.* **F.** *Cis* aff. *setifer.* **G.** *Cis* sp. E. **H.** *Cis* sp. F. **I.** *Cis* sp. G. Scale bars: 0,5 mm.

Figure 6. J. *Cis* sp. H. **K.** *Cis kawanabei.* **L.** *Cis pallidus.* **M.** *Cis pubescens.* **N.** *Falsocis brasiliensis.* **O.** Gen. nov. sp. 1. **P.** *Grossicis diadematus.* **Q.** "*Lipedanicis*" sp. 1. **R.** "*Lipedanicis*" sp. 2. Scale bars: 0,5 mm.

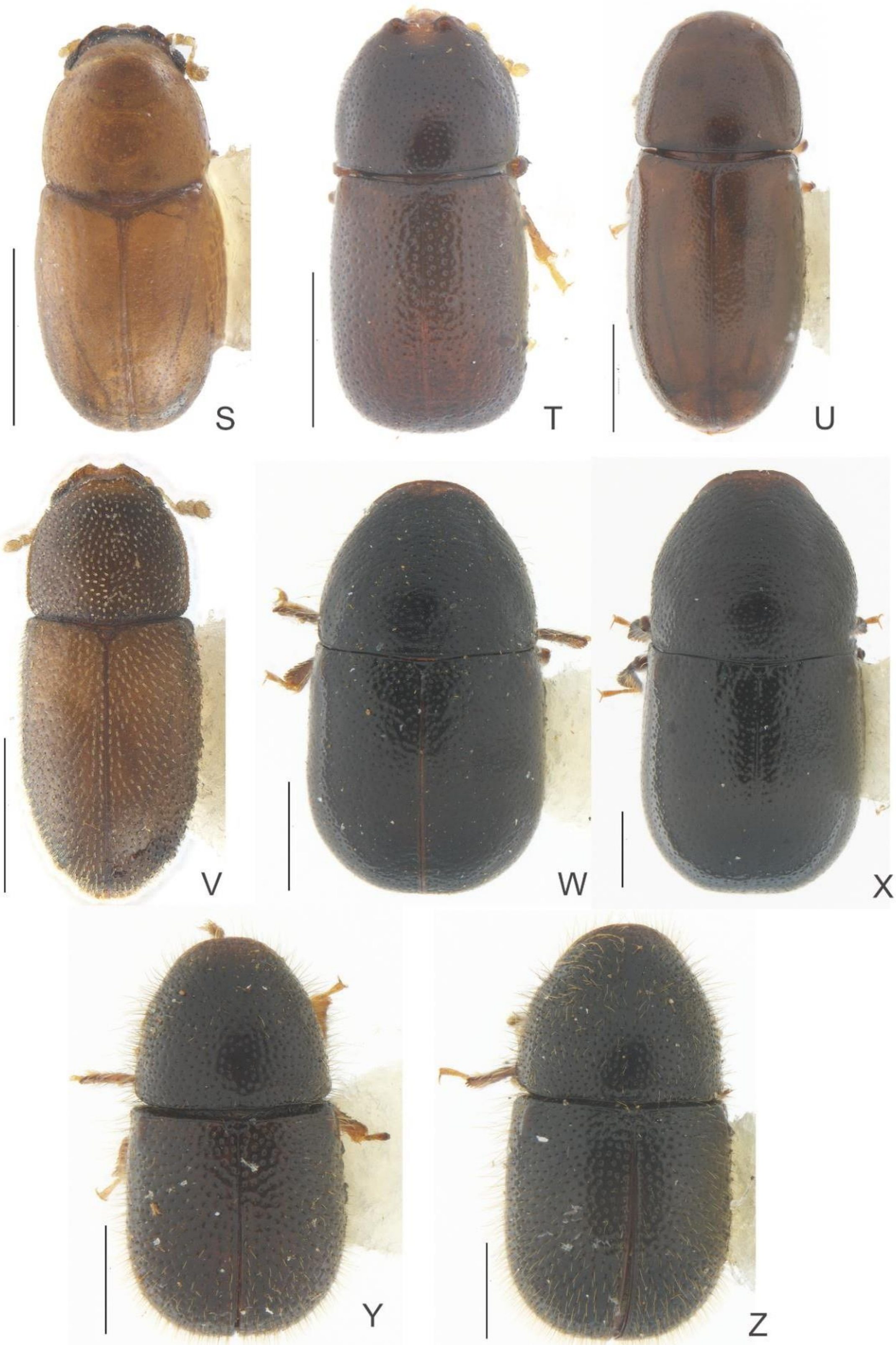

Figure 7. S. "*Lipedanicis*" sp. 3. **T.** *Phellinocis romualdoi.* **U.** *Porculus dufaui.* **V.** *Strigocis vicosensis.* **W.** *Xylographus contractus.* **X.** *Xylographus corpulentus.* **Y.** *Xylographus* sp. A. **Z.** *Xylographus* sp. B. Scale bars: 0,5 mm.

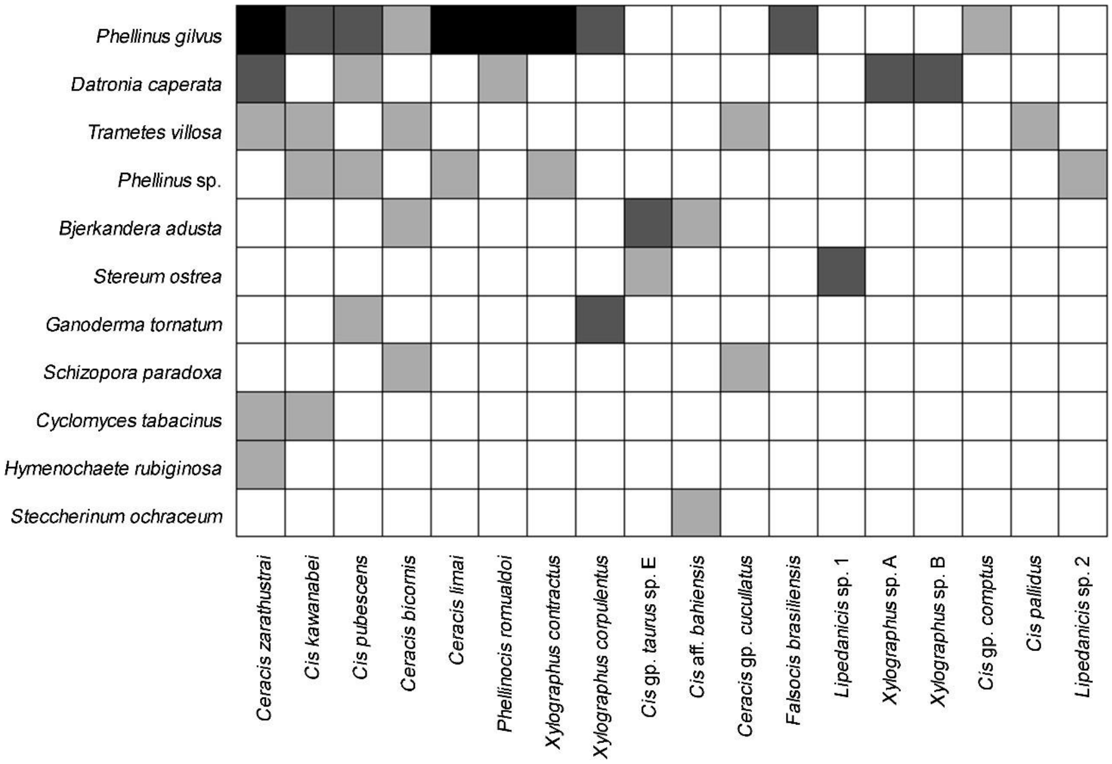

Figure 8. Occurrence matrix of Ciidae beetles in the host fungi at Mata da Biologia. The grayscale squares represent the frequency of occurrence of ciid species (black indicates higher frequency and light gray lower frequency; white indicates no occurrence).

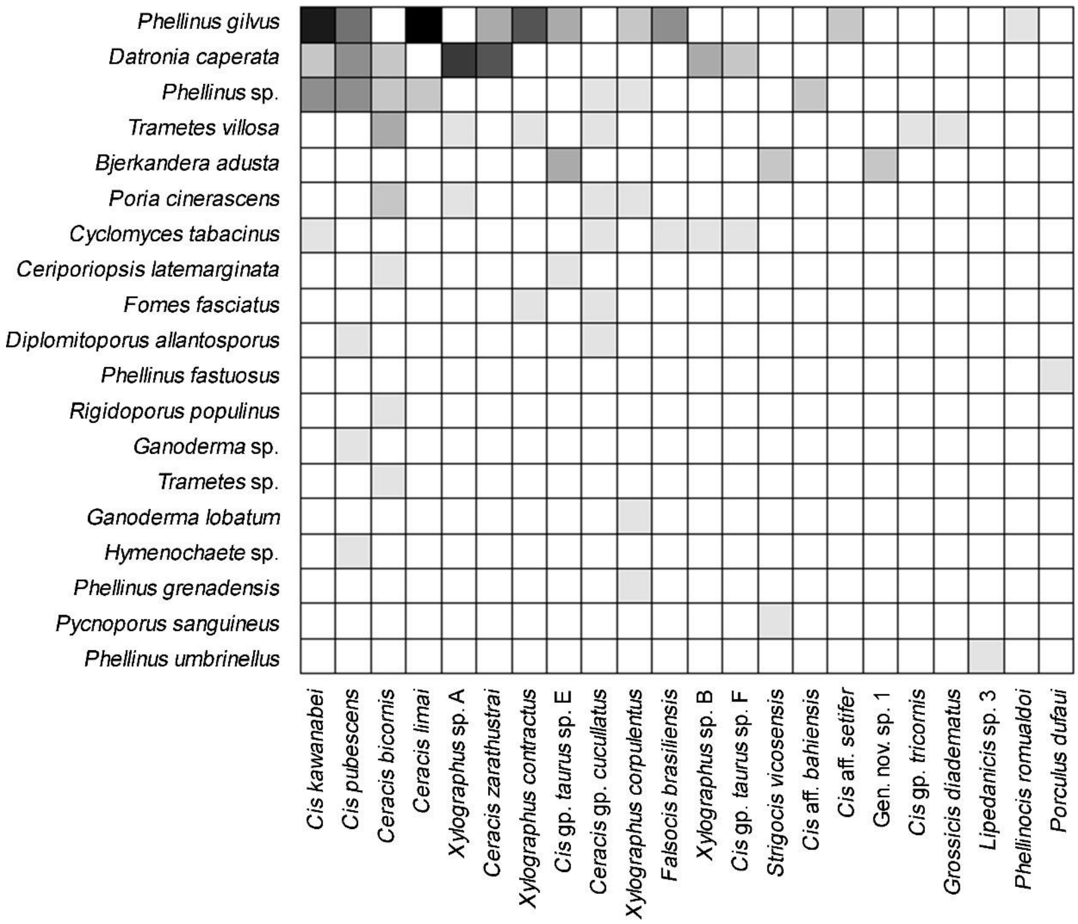

Figure 9. Occurrence matrix of Ciidae beetles in the host fungi at Mata do Paraíso. The grayscale squares represent the frequency of occurrence of ciid species (black indicates higher frequency and light gray lower frequency; white indicates no occurrence).

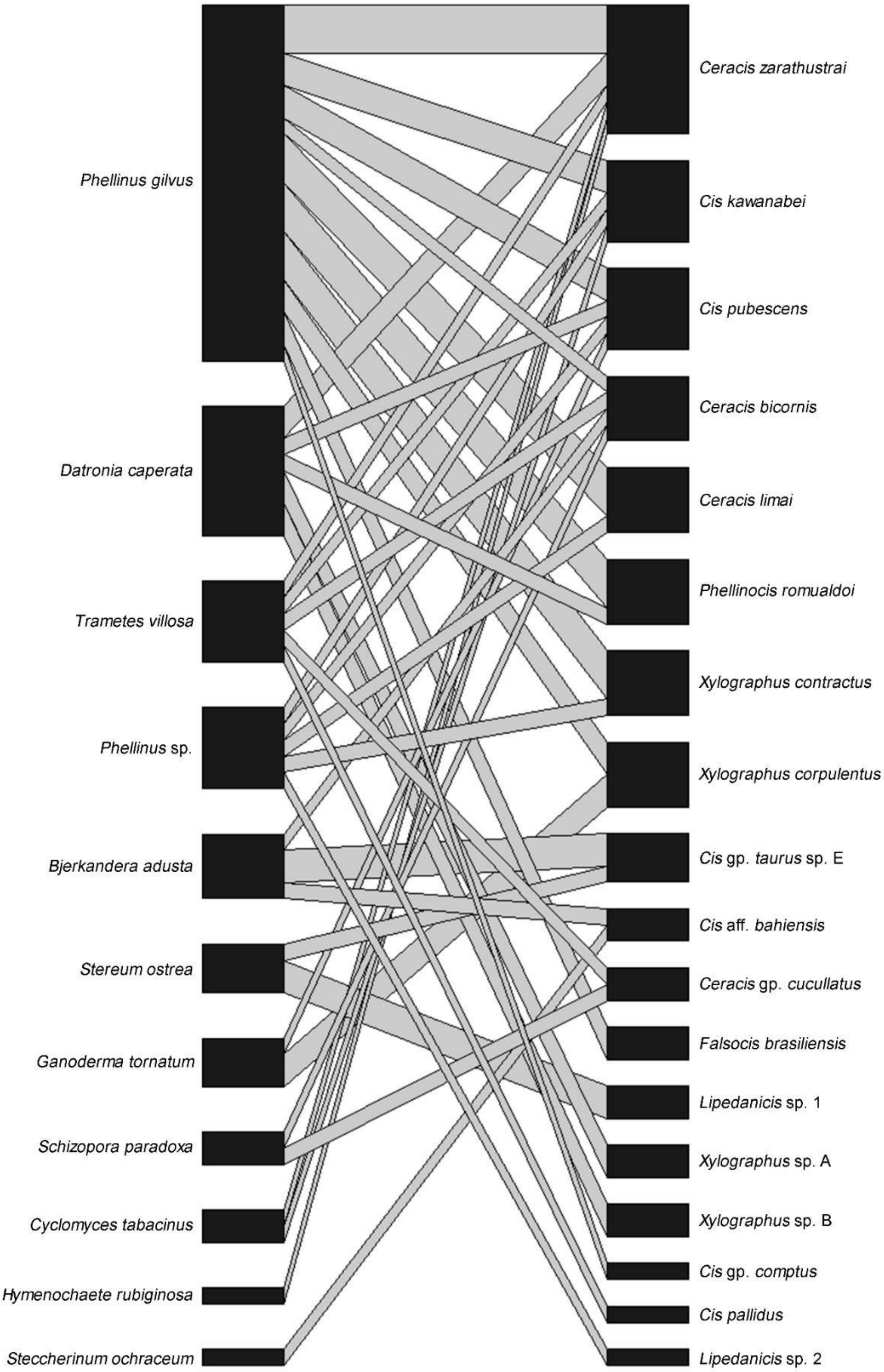

Figure 10. Interaction network between Ciidae species (right) and their fungal hosts (left) at Mata da Biologia (the size of the rectangles and lines represents the number of interactions).

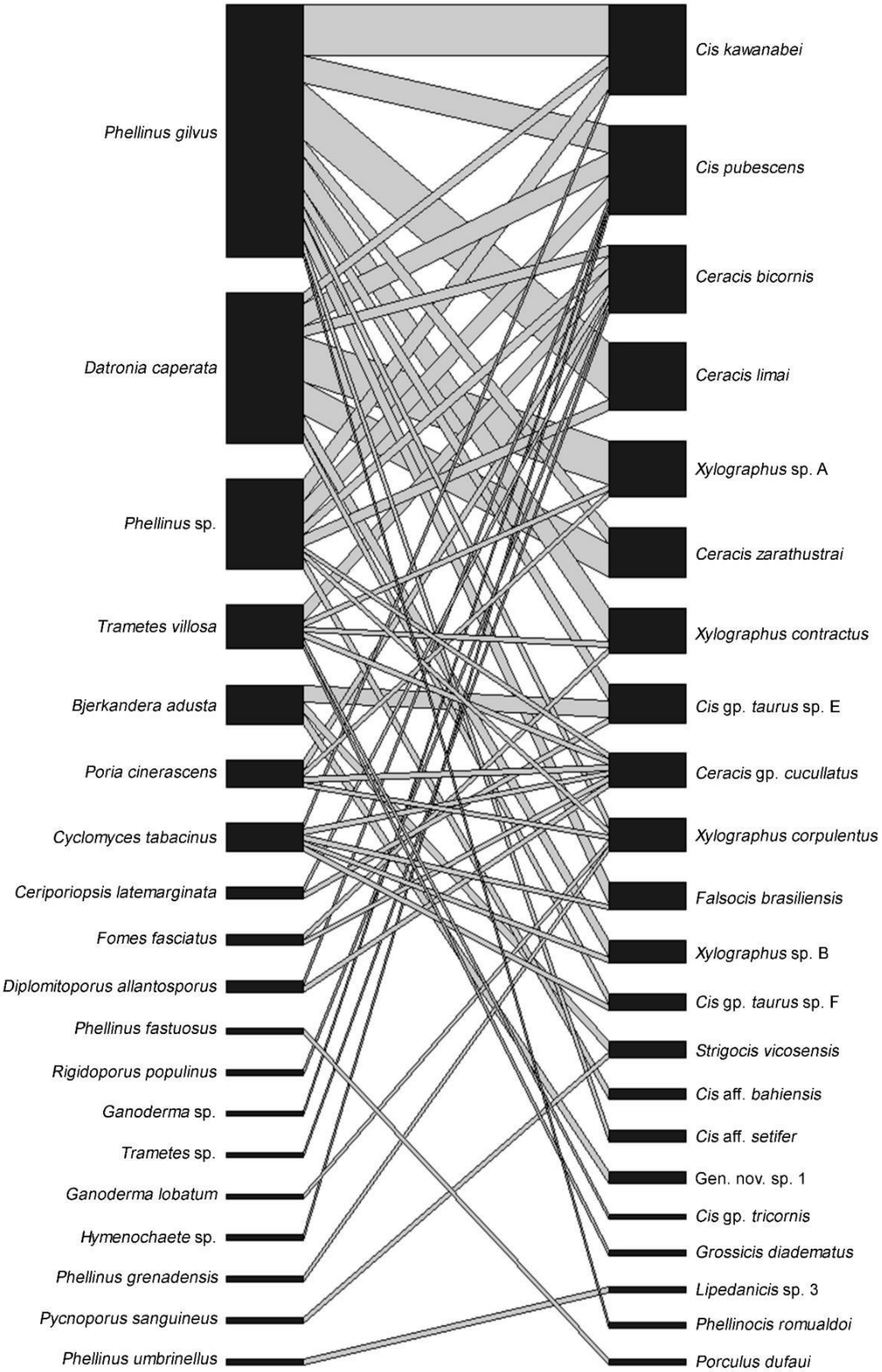

Figure 11. Interaction network between Ciidae species (right) and their fungal hosts (left) at Mata do Paraíso (the size of the rectangles and lines represents the number of interactions).

DISCUSSION

The ciids and fungi communities of MB and MP are different in species composition and, thus, distinct interactions networks are stablished in these forest remnants. It is known that the diversity of fungus species, and consequently the associated ciid species, are affected by size and connectivity of forested areas in a fragmented landscape (ARAUJO *et al.*, 2015). The two remnants sampled for the present work have very distinct sizes, and the smallest one (MB) is clearly more affected by edge effect.

The strong edge effect at the MB, due to its small area, directly affect the diversity of tree species (MURCIA, 1995), which in turns restrict the availability and quality of resources used by the associated fungi, reducing the species richness of the latter. Aside from the edge effect at the MB, we have also observed soil erosion within the remnant. That may be a consequence of the exploitation of the area in the past (as pasture and coffee plantation), followed by natural forest regeneration but with constant anthropic interference (the remnant is within a university campus, adjacent to the city downtown and is easily accessed by anyone). The resulting low species richness of tree-fungi may explain the low specialization of ciid species in the community, in which the most abundant fungi are used by the majority of ciid species. The least frequent ciid species (e.g. *C. pallidus*, *Cis* sp. G e "*Lipedanicis*" sp. 2) use the most common host fungi and had high cooccurrence to other ciid species. And the least used fungi, in their majority, are used by the most generalist ciid species.

At the MP, we observed a comparatively greater species richness of fungi, probably because this remnant suffers less from edge effect, as it is partially surrounded by adjacent forest remnants. The availability of more host fungal species probably has led to the distinct ciid-host associations observed in the remnants, in which the ciid species are more specialized to their hosts compared to the MB.

In our work, host fungi most used by the majority of ciid species were those shared by both remnants (*Bjerkandera adusta*, *Cyclomyces tabacinus*, *Datronia caperata*, *Phellinus gilvus*, *Phellinus* sp. and *Trametes villosa*). However, we observed distinct patterns of host use within each remnant, as revealed by the interaction networks (Figs 3, 4).

The connectance was greater at the MB (0.19) than at the MP (0.14), suggesting less specialization of ciid species in the former. The lowest connectance value of the MP may be a consequence of sample size, which increases in large networks with a greater number of less frequent species (BLÜTHGEN, 2010), as the MP has a greater number of exclusive species. Web asymmetry was also higher at the MB (0.24), a consequence of the lower fungal diversity, which may have led to a greater cooccurrence of ciid species in the fungal host species. That may also explain the lower degree of specialization of ciid species of the MB in comparison to those of the MP (BLÜTHGEN *et al.*, 2007).

Low degrees of specialization can increase the robustness of ecological communities (JACOBSEN *et al.*, 2018), a possible explanation to the higher robustness of the higher trophic level in the MB community. In contradiction, we observed that the nestedness index was higher in the MP, suggesting a greater vulnerability of the MB network to species loss (JACOBSEN *et al.*, 2018), which may also be related to the lower diversity of fungal species in this community. However, the nestedness index of the two communities was low, demonstrating the absence of a significantly nested pattern of interactions. Non-nested structures have been observed more frequently in quantitative (weighted) networks than in qualitative (binary) networks (JACOBSEN *et al.*, 2018; STANICZENKO *et al.*, 2013). Toju *et al.* (2015) suggested studying whether this “antinested” pattern is common in networks involving fungi, as a result of the great competition for substrate that occurs between these organisms.

Some of the collected ciid species, in both MB and MP, are usually found only in well-preserved forests, such as *Ce. limai*, *Ce. zarathustrai*, *F. brasiliensis* and *Phellinocis romualdoi*

(GRAF-PETERS *et al.*, 2011; LOPES-ANDRADE & LAWRENCE, 2005, 2011; PECCI-MADDALENA *et al.*, 2014). But their occurrence at the MB doesn't mean necessarily that the remnant is well preserved. MB and MP are within a very fragmented landscape of the Atlantic Forest biome, but they're very close to each other, being only 4,9 Km apart, with several other small forest remnants in between them. The largest remnant of this landscape (Viçosa and its surroundings) is MP, and it may act as a source of species for small remnants nearby, including MB. The Ciidae fauna of these small remnants may constantly receive dispersing ciids from MP, and forest-dependent species like *F. brasiliensis* and other mentioned above may persist in the landscape as metapopulations, but still depending on the availability of host-fungi and adequate conditions. The low quality of MB is denounced by the presence of ciid species usually associated with anthropized open areas, like *C. pallidus* and *Cis* sp. G (gp. *comptus*) (BORLINI *et al.*, 2018; DE ALMEIDA & LOPES-ANDRADE, 2004), the absence of other forest-depended ciids, such as *Cis* sp. H*, G. diadematus* and *Po. dufaui*, and the comparatively lower number of host fungus species. Note, for instance, that the host fungus *Trametes villosa* used by *Cis* sp. H and *G. diadematus* occurs at both MB and MP, but these ciid species were collected by us only at MP. It is interesting to note there are records of *G. diadematus* from 1999 to 2013 and a single collection of *Cis* sp. H at MB, but afterwards these species were not recollected at MB (ANTUNES-CARVALHO *et al.*, 2012; C. Lopes-Andrade pers. obs.). In the present survey, *Po. dufaui* occurred only in the host fungus *Phellinus fastuosus*, found only at MP; this species has two records at MB in 2001 and 2010, but was never recollected there afterwards (C. Lopes-Andrade *pers. obs.*). In the other hand, at MP, *Po. dufaui* has been consistently collected at least since 2010 (C. Lopes-Andrade, pers. obs.).

The Neotropical region encompasses very distinct biomes, usually with very high biodiversity of fungi and associated insects and proportion of endemic species (GUEVARA & DIRZO 1999; TUNDISI & MATSUMURA-TUNDISI, 2008). However, the study of insect-fungus associations within the region is still incipient, especially of Ciidae and the bracket fungi they use as hosts (DELGADO-CASTILLO & NAVARRETE-HEREDIA, 2011; GRAF *et al.*, 2018). The main cause of this situation is the lack of accessible and user-friendly identification keys for the macrofungi of most Neotropical biomes, and the same for the fauna of associated insects. Even in well-studied areas, as the forest remnants surveyed here, with continuous field collections of Ciidae ant their hosts since 1999, new species and even new genera of ciids may still be found, and we still face difficulties in identifying their fungal hosts. It's worth emphasizing the collection of the morphospecies called "Gen. nov. sp.1", which was never collected before in Viçosa and of which no other species is known from major museum collections of Ciidae in the world (C. Lopes-Andrade pers. obs.).

Our results showed that most Ciidae species are generalists and use host fungi according to their availability. Our collections took place in the rainy season, when most of the basidiomes were still growing. Jonsell and Nordlander (2004) showed that most specialist fungivorous insects, including ciids, used young and immature basidiomes, while most generalists used mature or deteriorated basidiomes. This suggests that the level of specialization in the network may vary, according to the deterioration of the fungi that make up the community. In view of this, in future works, it would be interesting to collect at different times of the year to obtain basidiomes in different stages of decomposition.

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FIGURES AND TABLES

Table 1. List of Ciidae species collected in each forest remnant. Abbreviations: MB – Mata da Biologia; MP – Mata do Paraíso.

Ciid species	**Remnant**
Ceracis bicornis (Mellié, 1849) (gp. *cucullatus*)	MB / MP
Ceracis sp. 1 (gp. *cucullatus*)	MB / MP
Ceracis limai Lopes-Andrade et al., 2002 (gp. *singularis*)	MB / MP
Ceracis zarathustrai Pecci-Maddalena et al., 2014	MB / MP
Cis aff. *bahiensis* (Pic, 1916) (gp. *taurus*)	MB / MP
Cis aff. *setifer* (Gorham, 1883) (gp. *taurus*)	MP
Cis sp. E (gp. *taurus*)	MB / MP
Cis sp. F (gp. *taurus*)	MP
Cis sp. G (gp. *comptus*)	MB
Cis sp. H (gp. *tricornis*)	MP
Cis kawanabei Lopes-Andrade, 2002 (gp. *taurus*)	MB / MP
Cis pallidus Mellié, 1849 (gp. *pallidus*)	MB
Cis pubescens (Friedenreich, 1881) (gp. *taurus*)	MB / MP

Falsocis brasiliensis Lopes-Andrade, 2007	MB / MP
Gen. nov. sp. 1	MP
Grossicis diadematus (Mellié, 1849)	MP
"*Lipedanicis*" sp. 1	MB
"*Lipedanicis*" sp. 2	MB
"*Lipedanicis*" sp. 3	MP
Phellinocis romualdoi Lopes-Andrade & Lawrence, 2005	MB / MP
Porculus dufaui (Pic, 1922)	MP
Strigocis vicosensis Lopes-Andrade, 2011	MP
Xylographus contractus Mellié, 1849	MB / MP
Xylographus corpulentus Mellié, 1849	MB / MP
Xylographus sp. A	MB / MP
Xylographus sp. B	MB / MP

Table 2. List of fungus species collected in each forest remnant. Abbreviations: MB – Mata da Biologia; MP – Mata do Paraíso.

Order	**Family**	**Fungi species**	**Locality**
Hymenochaetales	Hymenochaetaceae	*Cyclomyces tabacinus* (Mont.) Pat., 1900	MB / MP
		Hymenochaete rubiginosa (Dicks.) Lév.,1846	MB
		Hymenochaete sp.	MP
		Phellinus fastuosus (Lév.) S. Ahmad, 1972	MP
		Phellinus gilvus (Schwein.) Pat., 1900	MB / MP
		Phellinus grenadensis (Murrill) Ryvarden, 1972	MP
		Phellinus sp.	MB / MP
		Phellinus umbrinellus (Bres.) S. Herrera & Bondartseva, 1980	MP
	Schizoporaceae	*Rigidoporus populinus* (Schumach.) Pouzar, 1966	MP

		Schizopora paradoxa (Schrad.) Donk, 1967	MB
Polyporales	Meruliaceae	*Bjerkandera adusta* (Willd.) P.Karst., 1879	MB / MP
		Ceriporiopsis latemarginata (Rick) Rajchenb., 1987	MP
	Polyporaceae	*Ganoderma lobatum* (Cooke) G. F. Atk., 1908	MP
		Ganoderma sp.	MP
		Ganoderma tornatum (Pers.) Bres., 1912	MB
		Datronia caperata (Berk.) Ryvarden, 1985	MB / MP
		Diplomitoporus allantosporus Ryvarden & Iturr., 2003	MP
		Fomes fasciatus (Sw.) Cooke, 1885	MP
		Poria cinerascens Sacc. & P. Syd., 1902	MP
		Pycnoporus sanguineus (L.) Murrill, 1904	MP
		Trametes sp.	MP
		Trametes villosa (Sw.) Kreisel, 1971	MB / MP
	Steccherinaceae	*Steccherinum ochraceum* (Pers.) Gray, 1821	MB
Russulales	Stereaceae	*Stereum ostrea* (Blume & T. Nees) Fr.,1838	MB

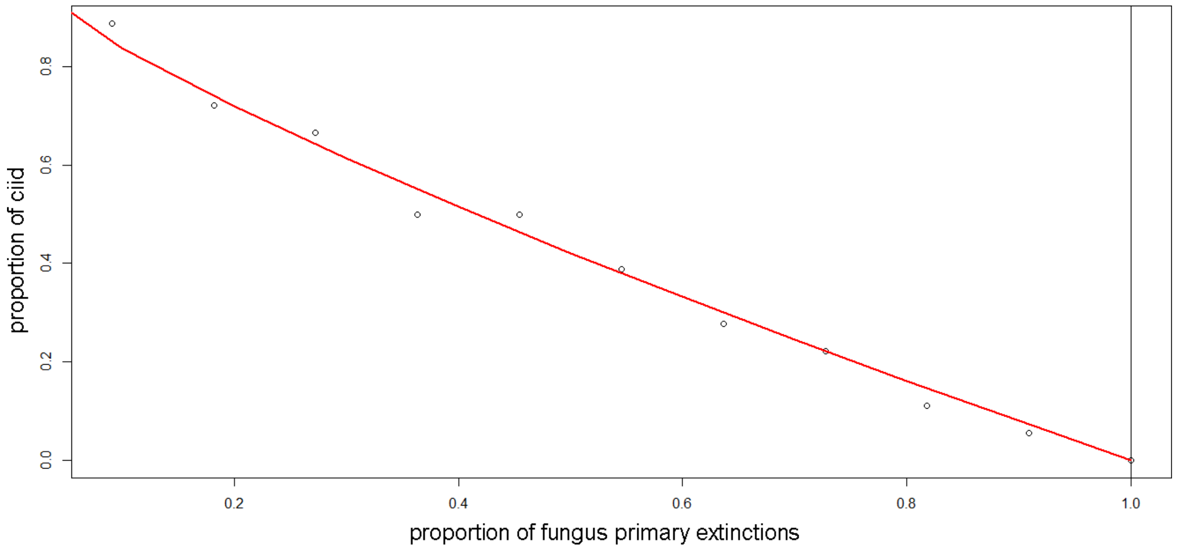

Figure 12. Proportion of ciid species loss due to the loss of fungal species with more links at Mata da Biologia (circles represent the loss of fungi species and the red line represents the estimated loss of ciid species).

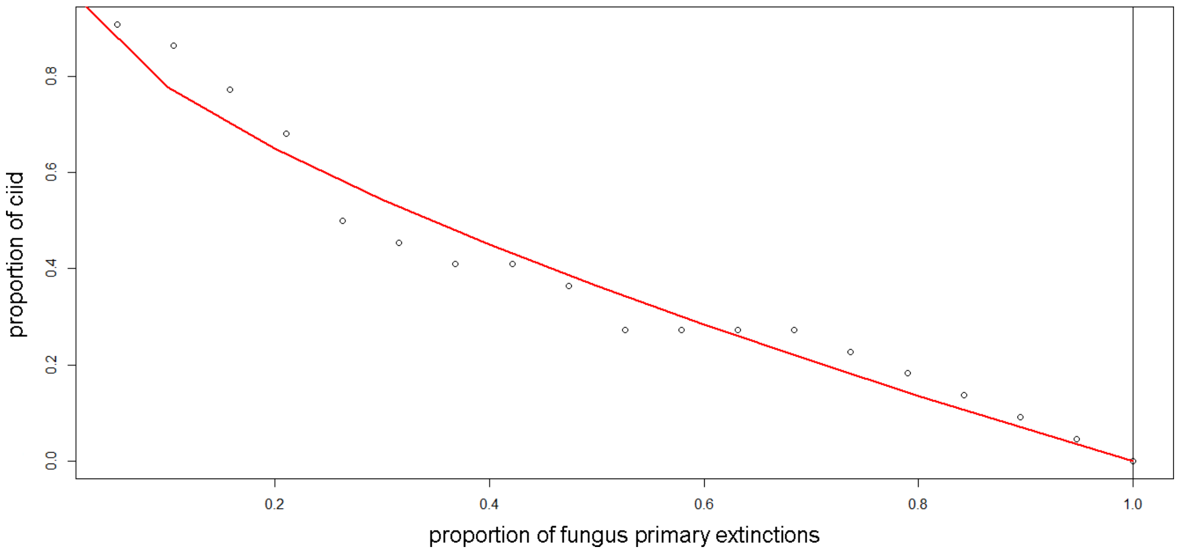

Figure 13. Proportion of ciid species loss due to the loss of fungal species with more links at Mata do Paraíso (circles represent the loss of fungi species and the red line represents the estimated loss of ciid species).